Neuropsychologia 104 (2017) 113–125

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Semantic control deficits impair understanding of thematic relationships more than object identity

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ARTICLE INFO

Keywords:
Semantic
Control
Aphasia
Stroke
Thematic

ABSTRACT

Recent work has suggested a potential link between the neurocognitive mechanisms supporting the retrieval of events and thematic associations (i.e., knowledge about how concepts relate in a meaningful context) and semantic control processes that support the capacity to shape retrieval to suit the circumstances. Thematic associations and events are inherently flexible: the meaning of an item changes depending on the context (for example, lamp goes with reading, bicycle and police). Control processes might stabilise weak yet currently-relevant interpretations during event understanding. In contrast, semantic retrieval for objects (to understand what items are, and the categories they belong to) is potentially constrained by sensory-motor features (e.g., bright light) that change less across contexts. Semantic control and event understanding produce overlapping patterns of activation in healthy participants in left prefrontal and temporoparietal regions, but the potential causal link between these aspects of semantic cognition has not been examined. We predict that event understanding relies on semantic control, due to associations being necessarily context-dependent and variable. We tested this hypothesis in two ways: (i) by examining thematic associations and object identity in patients with semantic aphasia, who have well-documented deficits of semantic control following left frontoparietal stroke and (ii) using the same tasks in healthy controls under dual-task conditions that depleted the capacity for cognitive control. The patients were impaired on both identity and thematic matching tasks, and they showed particular difficulty on non-dominant thematic associations which required greater control over semantic retrieval. Healthy participants showed the same pattern under conditions of divided attention. These findings support the view that semantic control is necessary for organising and constraining the retrieval of thematic associations.

1. . Introduction

Across our lifetime we acquire rich and varied conceptual knowledge, making it necessary to constrain retrieval so that it is focussed on only the information that is relevant for the current task or context (Badre et al., 2005; Jefferies, 2013; Noonan et al., 2010). We have knowledge about what *objects* are and the categories they belong to (e.g., *taxonomic knowledge* – identifying that an animal that barks, has a wet nose and has spots is a DALMATIAN), as well as *thematic knowledge* of how objects are used and how they relate to other objects in the context of *events* (e.g., associating SPOON with SUGAR in the context of drinking tea, even though these objects do not share physical features). This knowledge needs to be stored and accessed in a context-flexible manner. The neural organisation of these different facets of semantic cognition – both the distinction between object and event knowledge, and between conceptual representations and control processes – remains highly controversial. These are set out in two parallel lines of literature, proposing (1) two distinct storage hubs for object and event knowledge (Schwartz et al., 2011) and (2) a heteromodal conceptual hub integrating information within modality-specific spokes, plus executive-access mechanisms that shape the information that is retrieved so that it is relevant to the current task or context (Lambon Ralph et al., 2017). These accounts propose alternative roles for similar brain areas, yet there have been few attempts to directly compare them. Here we investigate whether differences between object and thematic knowledge might be partially explained in terms of their reliance on semantic control processes.

Some researchers have proposed *two separate hubs* for taxonomic and thematic knowledge, in the anterior temporal lobe (ATL) and temporoparietal cortex respectively (Binder and Desai, 2011; Kalénine

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http://dx.doi.org/10.1016/j.neuropsychologia.2017.08.013
Received 13 March 2017; Received in revised form 13 June 2017; Accepted 7 August 2017
Available online 11 August 2017

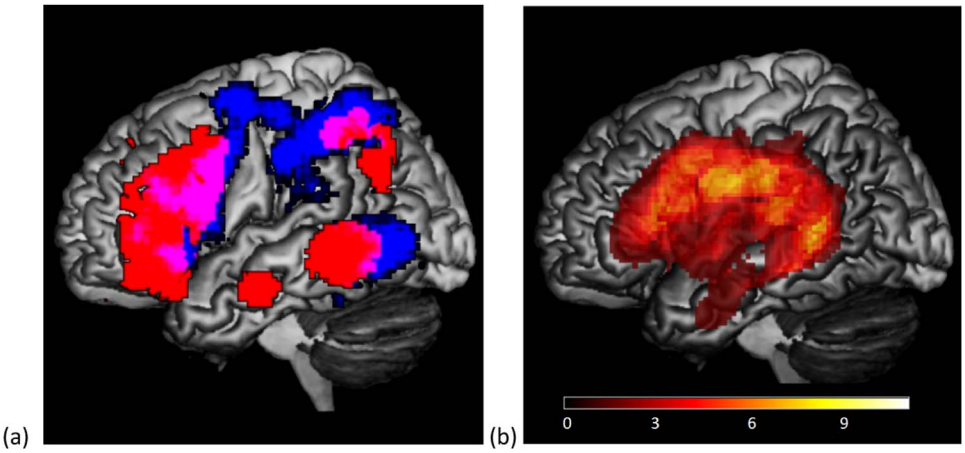

Fig. 1. (a) overlap of semantic control regions (red), taken from Noonan et al. (2013); and 'action' regions (blue), taken from an automated meta-analysis of 708 studies using Neurosynth (http://neurosynth.org/). The overlap of the control and action regions is in pink (in pMTG, anterior IPL, premotor cortex and posterior IFG). (b) SA lesion overlay map showing areas of maximum overlap (11 patients in total). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

et al., 2012; Kalénine et al., 2013; Schwartz et al., 2011; Solène and Buxbaum, 2016). Neuropsychological evidence for this view is provided by picture naming errors, with damage to the ATL associated with category co-ordinate or superordinate errors (e.g., APPLE – "fruit") and temporoparietal damage associated with thematic errors, such as responding "nuts" to a picture of SQUIRREL (Jefferies et al., 2008; Schwartz et al., 2011). This pattern has been argued to reflect perturbation of distinct types of knowledge following damage to dissociable areas of cortex. The two hub account has also received support from neuroimaging studies showing greater activity in posterior temporal and/or parietal regions in response to thematic judgments (de Zubicaray et al., 2013; Kalénine et al., 2009). Temporoparietal regions are consistently responsive to praxis, visual motion, actions and motor planning (Martin, 2007; Noppeney, 2008). These regions might therefore be well-placed to support the comprehension of events and thematic associations. Equally, the ATL is at the end of the ventral visual stream, and it has been previously associated with the integration of featural knowledge (Bemis and Pylkkanen, 2011; Moss et al., 2005).

However, a number of fMRI investigations have failed to find a distinction between thematic and categorical knowledge in these proposed hub regions (Jackson et al., 2015; Kotz, 2002; Sachs et al., 2008; Sass et al., 2009). Experimentally, it is difficult to entirely separate tasks on the basis of identity or thematic knowledge, since thematic tasks necessarily involve identifying what objects are, while items drawn from the same category (e.g., DOG and SHEEP) almost always share thematic associations (Jackson et al., 2015). Moreover, an alternative hypothesis, the Controlled Semantic Cognition framework (Lambon Ralph et al., 2017), does not distinguish knowledge by its nature (thematic or taxonomic), but by its *accessibility*. By this view, the ATL is thought to form a central semantic hub encompassing multiple aspects of knowledge (Lambon Ralph et al., 2017; Patterson et al., 2007). Patients with semantic dementia (SD), who have relatively focal degeneration of the ATL bilaterally (Mummery et al., 2000), show highly consistent errors for the same concepts across different tasks – including across object matching and thematic matching paradigms (Bozeat et al., 2000; Hoffman et al., 2013; Jefferies and Lambon Ralph, 2006), consistent with degradation of core conceptual knowledge that encompasses both the physical and associative features of items. The semantic deficit in SD erodes the distinction between specific concepts first, such that patients can no longer distinguish a DALMATIAN from other breeds of dog; but can identify that this item is an animal (Hodges and Patterson, 2007; Mummery et al., 2000; Rogers et al., 2006). ATL is thought to integrate modality-specific features, allowing deep conceptual similarities and distinctions to be extracted (the "hub and spoke model"; Patterson et al., 2007; Rogers et al., 2006; Rogers et al., 2004). There is also growing evidence from distortion-corrected and distortion-limiting fMRI methods and transcranial magnetic stimulation studies that the ventral ATL is involved in multimodal semantic processing in healthy participants, in line with this view (Binney et al., 2010; Pobric et al., 2010; Visser et al., 2012).

The Controlled Semantic Cognition account proposes that semantic knowledge interacts with control processes to allow appropriate semantically-driven thoughts and behaviour (Lambon Ralph et al., 2017; Jefferies, 2013). Consequently, when distinctions between types of knowledge (thematic or taxonomic) occur, these may stem from differences in accessibility or control requirements. Thematic judgments are contextually-guided: there are diverse associations to any given concept and thus it is necessary to shape retrieval to focus on the specific links that are relevant to a particular situation: for example, the word LAMP may be associated with BICYCLE but also with READING, depending on the circumstances. A common network of brain regions including left inferior frontal gyrus (IFG) and posterior middle temporal gyrus (pMTG) is implicated in situations in which semantic cognition is relatively controlled, i.e., during the retrieval of ambiguous word meanings and weak semantic relationships (Davey et al., 2016; Noonan et al., 2013; Whitney et al., 2011), and also in understanding events, actions and thematic associations (de Zubicaray et al., 2013; Kalénine et al., 2013; Mirman and Graziano, 2012). For example, a recent study found overlapping voxels within both left IFG and pMTG for contrasts examining action understanding and semantic control when these were manipulated within a single study in the same participants (Davey et al., 2015b; see also Fig. 1 below). Left IFG and pMTG are key components of a large-scale network activated by diverse manipulations of semantic control demands in an activation-likelihood meta-analysis (Noonan et al., 2013) and the co-activation of these regions has also been observed in individual studies (Davey et al., 2016). Moreover, TMS to both regions produces an equivalent disruption of tasks requiring semantic control but not more automatic semantic association judgements (Davey et al., 2015a; Whitney et al., 2011). Together, these findings suggest that related and overlapping brain networks might support both semantic control and the retrieval of thematic or event knowledge. This overlap might reflect the inherent flexibility of thematic associations, actions and events: when making judgements to these kinds of stimuli, there is a need to flexibly prioritise different features within the long-term semantic store depending on the context in which concepts occur. Control processes might help to stabilise weak yet currently-relevant interpretations in these kinds of tasks: for example, they may promote particular associations that are relevant to the link with a target word, or potential action features of objects that allow an item to be used in a particular way, which is suited to the context. In contrast, semantic tasks focussed on object identity and categorical distinctions may be more constrained by sensory-motor features (e.g., LAMPS have a bright light and they can be categorised with other objects with this property, such as TORCH): these core features arguably change less across contexts (although such features are not always present, and physical features such as size and colour can also be